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Concentrations and standing crops of calcium, magnesium, potassium and sodium in soil and litter arthropods and their food in an aspen woodland ecosystem in the Rocky Mountains (Canada)

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With 1 figure

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1. Introduction

In studies on the roles of particular organisms in chemical cycling it is essential to know the chemical content of the organisms and of their food. Such data together with biomass estimates and rates of chemical turnover can then be used to describe chemical flux by the consumer organisms. At present there are few data of this type available for North American terrestrial ecosystems. In south-eastern U.S.A., Reichle et al. (1969), van Hook (1971), Gist (1972) and McBrayer et al. (1974) have reported concentrations of certain chemical elements in invertebrates and the last three authors, in studies of chemical cycling, also reported data on chemical standing crops. Chemical data on bacteria and on fungi were described by Todd et al. (1973), Ausmus and Witkamp (1974) and Cromack et al. (1975). Chemical data for fungi in a Jeffrey Pine ecosystem in Nevada were described by Stark (1973). Outside of North America, Grimshaw et al. (1958) have reported on the concentrations of chemical elements in insects in an English pine stand.

The objectives of this study were to extend our knowledge of North American ecosystems by investigating the concentrations and standing crops of calcium, magnesium, potassium and sodium in soil invertebrates and their surroundings in an aspen woodland ecosystem in the northern Rockies (Canada).

2. Study area

The study area was in the Kananaskis Valley of Alberta (ca. 51° 02′ N, 115° 02′ W; altitude 1400 m) and is described in detail elsewhere (Mitchell 1974; Loubier 1974). Aspen poplar (*Populus tremu-*

loides MICHX.) was the major species with some balsam poplar (*P. balsamifera* L.). The climate is characterized by short summers and relatively long winters with intermittent warm winds. The soil was generally frozen from mid-November to mid-April.

3. Methods

3.1. Sampling and extraction of soil invertebrates

Microarthropods were quantitatively sampled by soil cores (22.9 cm^2 surface area) taken in August and September 1973 and May, June and September in 1974. Organisms were extracted from the cores by simple Tullgren funnels (plastic with 60 W bulbs) over a period of three days and also by Macfadyen high gradient extraction units over periods of five days. In the former method, the cores were fragmented before being placed in the funnels, while in the latter method the cores were separated into 2.5 cm layers and each layer placed intact into the extraction unit (after MITCHELL 1974). Specimens for chemical analyses were extracted into double distilled water.

Carabid beetles were sampled by removing litter, humus and bark from areas of 1 m^2 in the aspen woodland. Sampling positions were determined by pairs of random numbers. Larvae and adults of the carabid *Agonum retractum* Leconte were sampled regularly so as to provide material for the study of chemical variation within and between different age groups of this species. Beetles were extracted in controlled draught Tullgren funnels (MACFADYEN 1962) over periods of two days for adults and three days for larvae. Adults were also collected from pitfall traps (modified flower pots, 15 cm in diam.).

Other macroarthropods (millipedes, centipedes, lepidopterous and dipterous larvae) were hand-collected from under logs, from pitfall traps and extracted from soil and litter placed in Tullgren funnels, as described above for carabid adults.

3.2. Analysis of chemical elements

Plant and animal material were analyzed for calcium, magnesium, potassium and sodium on a Perkin-Elmer 303 Atomic Absorption Spectrophotometer in the Environmental Sciences Centres laboratory. Samples were dried for four days at 65 °C and then weighed on a Cahn Gram Electrobalance before digestion with 30 % perchloric acid and 70 % nitric acid.

REICHLE et al. (1969) observed that the potassium content will be underestimated if samples are prepared at over 450 °C. In preliminary analyses, four insect samples were prepared using the REICHLE et al. (1969) method (digestion with HNO_3 and HCl prior to ashing in a muffle furnace) and four were acid digested only, as described above. Potassium concentrations in dry ashed samples were significantly lower than those in acid digested samples (Table 1). These results compare with

Table 1. The effect of sample preparation on results of chemical analysis of *Agonum retractum*

Sample preparation method	N	mg/g ($\bar{x} \pm 95\,\%$ confidence limits)			
		Calcium	Magnesium	Potassium	Sodium
Ashed prior to acid digestion	4	2.24 ± 2.09	0.92 ± 0.31	1.17 ± 0.66	3.23 ± 0.84
Acid digested only	4	2.23 ± 2.58	1.11 ± 0.78	4.63 ± 0.48	2.50 ± 1.84

those of GIST (1972) but not with those of GIRON (1973) who found no differences in potassium concentrations of samples dry ashed and acid digested only, although he obtained better precision with the former method. GIRON suggested that the variability in acid digested samples may have been caused by spattering of some of the samples during boiling. If this was so it would have been more of a problem with samples of large size; GIRON digested plant samples of 2 g each and the sample size used here was generally not greater than 0.025 g. As samples digested with acid contained higher potassium levels, this sample preparation method was used routinely.

4. Results

4.1. Chemical composition of consumers and their food

The chemical composition of consumers and of their food is summarized in Fig. 1. Magnesium concentrations are not included because high levels occurred only in leaves and in

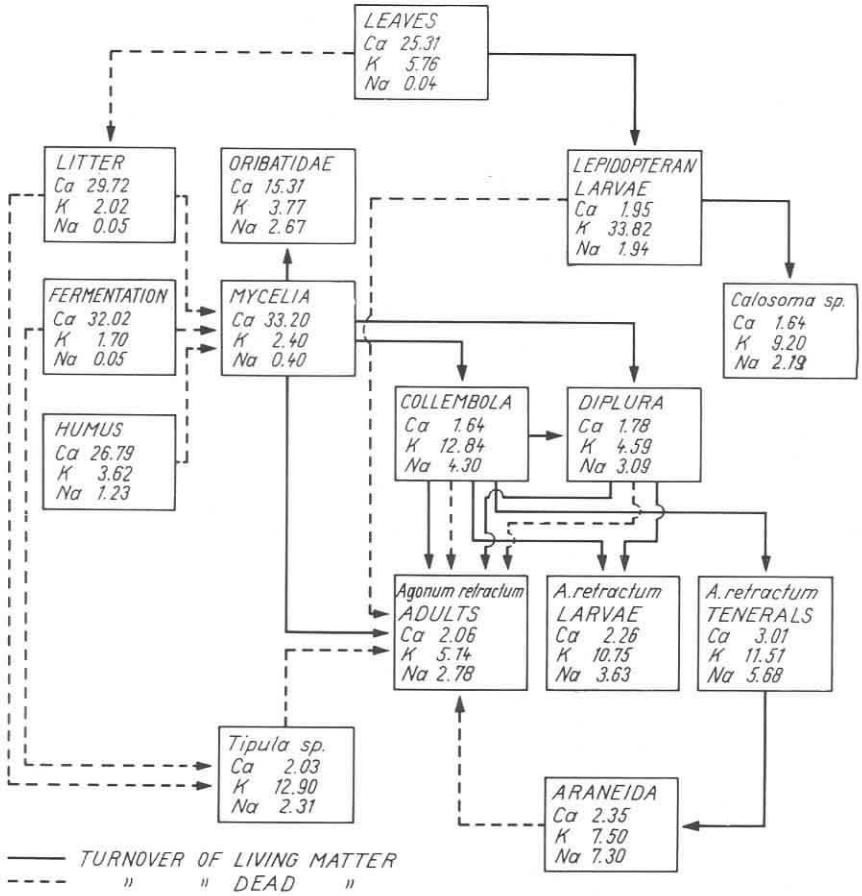

Fig. 1. Food web relationships of *Agonum retractum* and other organisms and their chemical concentrations (mg/g dry weight). Note. —FERMENTATION should be red FERMENTATION LAYER.

their primary consumers, lepidopterous larvae (Table 2). The chemical composition of the fermentation layer in the aspen soil (Table 2) was taken as a rough approximation of food concentrations of litter grazers such as dipterous larvae and millipedes. Adults and larvae of the carabid *Calosoma frigidum* Kirby preyed on lepidopterous larvae. Other adult carabids such as *Agonum retractum* were general predators on soft bodied organisms and were also necrophages while their larvae were probably general predators (CARTER 1975).

All consumers concentrated potassium and sodium over the concentrations found in living leaves, the fermentation layer and in fungal mycelia (Fig. 1). Lepidopterous larvae and basidiocarps had the highest potassium levels. Sodium concentrations followed the pattern: living leaves and soil horizons (with the exception of humus) < fungi < arthropods. LITTER grazers such as stratiomyid larvae and millipedes had highly calcareous exoskeletons and thus had high calcium concentrations while others such as *Tipula* sp. larvae had body concentrations similar to those of other arthropods examined, with the exception of the oribatid *Eupterotegaeus rostratus* (Table 2).

4.2 Seasonal changes in composition of *Agonum retractum*

Several samples of the population *Agonum retractum* were taken and so comparisons within and between years were possible. Calcium and magnesium levels in all stages ex-

Table 2. Chemical composition of soil, fungi and certain invertebrates in the aspen woodland ecosystem

	Total no. individuals analyzed	No. replicate determinations	mg/g dry weight ($\bar{x} \pm 95\%$ conficence limits)			
			Calcium	Magnesium	Potassium	Sodium
Leaves	—	6	25.31 ± 6.91	3.53 ± 0.78	5.76 ± 1.91	0.04 ± 0.023
Litter	—	21	29.72 ± 0.83	1.95 ± 0.004	2.02 ± 0.20	0.05 ± 0.045
Fermentation	—	21	32.02 ± 0.77	2.06 ± 0.07	1.70 ± 0.08	0.05 ± 0.015
Humus	—	21	26.79 ± 1.12	1.11 ± 0.32	3.62 ± 0.27	1.23 ± 0.090
Fungal mycelia*			33.20	1.9	2.4	0.4
Fungal fruiting bodies	—	8	1.38 ± 0.85	1.24 ± 0.30	29.97 ± 4.65	0.67 ± 0.44
Lepidopteran larvae (H)	6	6	1.95 ± 0.56	3.86 ± 0.50	33.52 ± 6.54	1.94 ± 1.76
Cryptostigmata						
Eupterotegaeus rostratus (M)	1124	1	15.31	1.82	3.77	2.67
Collembola						
Ceratophysella armata (M)	—	2	1.63 ± 1.02	2.04 ± 1.87	12.84 ± 4.29	4.30 ± 1.94
Dipteran larvae						
Tipula sp. (L)	6	4	1.52 ± 2.53	1.94 ± 2.45	12.90 ± 4.90	2.20 ± 3.14
Stratiomyid spp. (L)	8	1	95.05	2.17	7.68	0.54
Diplopoda (L)	14	2	121.78 ± 22.48	1.56 ± 1.38	4.30 ± 4.49	3.06 ± 6.82
Diplura (O)	—	1	1.78	1.60	4.59	3.09
Pseudoscorpions (P)	—	1	2.86	1.60	8.28	5.95
Centipedes (P)	6	1	1.83	0.72	5.35	5 65
Carabidae						
Agonum retractum (P, N)	300	23	2.06 ± 0.80	1.12 ± 0.15	5.14 ± 0.84	2.78 ± 0.28
Calathus ingratus (P, N)	8	3	1.06 ± 0.57	0.99 ± 0.05	8.02 ± 0.42	2.42 ± 0.37
Calosoma frigidum						
Adults (P)	3	3	1.64 ± 1.33	2.79 ± 4.03	9.20 ± 19.19	2.19 ± 1.63
Larvae (P)	3	3	1.44 ± 0.91	1.72 ± 0.55	9.06 ± 1.95	0.98 ± 1.18

* From Ausmus and Witkamp (1974)
Feeding types of arthropods are given in parentheses where H = herbivore, L = litter grazer, M = mycophage, N = necrophage, O = omnivore, and P = predator.

Table 3. Comparison of chemical elemental concentrations (mg/g dry wt) of certain soil invertebrates from studies in southeastern U.S. ecosystems and from the present study

	Calcium			Magnesium	Potassium			Sodium	
	1	2	3	3	1	2	3	1	3
Oribatid mites	—	35.00	15.31	1.82	—	5.60	3.77	—	2.67
Collembola	—	2.96	1.63	2.04	—	12.75	12.84	—	4.30
Carabids									
eggs	—	—	2.25	1.92	—	—	10.33	—	6.04
larvae	—	—	2.26	2.73	—	—	10.75	—	3.63
tenerals	—	—	3.01	3.63	—	—	11.51	—	5.68
old adults	0.70	6.00	2.06	1.12	2.62	7.00	5.58	4.25	2.87
males	—	—	2.54	1.15	—	—	5.68	—	3.02
females	—	—	1.57	1.10	—	—	5.47	—	2.72
Spiders	2.1	2.60	—	—	7.2	7.80	—	7.3	—
Lepidopterous larvae	4.7	—	1.95	3.86	50.0	—	33.52	9.2	1.94

1 = Reichle et al. 1969; 2 = Gist 1972; 3 = Present study

amined were similar. Potassium concentrations were highest in eggs, larvae and tenerals while sodium levels were highest in eggs and tenerals (Table 3).

Data for females in relation to reproduction and overwintering are included in Table 4. The chemical composition of males and females was similar (see Table 3). Only potassium concentrations changed significantly between sampling periods. Concentrations decreased after June of 1971 and 1974. In 1971 the decrease was correlated with the end of egg laying, but not in 1974 when females carried eggs after mid-July (Carter 1975). The wide variances of the 1972 samples were a consequence of the small number of samples available for that year.

4.3 Standing crops of chemical elements

Chemical standing crops of several of the organisms referred to above, and in their surroundings, are presented in Table 5. Standing crops of calcium, magnesium, potassium and sodium in soil fungi were based on biomass estimates of fungal mycelia obtained by Visser and Parkinson (1975) and may be compared with the standing crops in the soil horizons in Table 5.

Estimates of the contribution of different age groups to the chemical standing crop of the *Agonum retractum* population are summarized in Table 5 (from Carter and Pritchard, 1976). The standing crop was lowest before and during reproduction and maximal in autumn provided that teneral adults were numerous. In 1974, when tenerals were very rare (Carter, 1975), no marked change in the value of the standing crop occurred. *Calathus ingratus* was the carabid next in abundance to *A. retractum* but its numbers decreased between mid-1971 and 1974. Its mean biomass and chemical standing crop were similar to those of less abundant but heavier carabids, such as *Calosoma frigidum* (Table 5).

5. Discussion

Generally, chemical concentrations of consumers were independent of their feeding habits (Fig. 1) and appeared instead to be dependent on the biochemical and physiological characteristics of different taxa. Thus, predators such as centipedes and pseudoscorpions had high sodium concentrations in comparison with predaceous carabid adults and larvae such as those of *Calosoma frigidum*. Of the litter grazers analyzed, only stratiomyid larvae had very low sodium levels. Litter grazers with highly calcareous exoskeletons had by far the highest calcium concentrations.

In a few arthropods, high chemical concentrations were correlated with high concentrations in their food. High potassium and magnesium levels were found in lepidopterous larvae

Table 4. Chemical composition of adult females of *Agonum retractum*

		Total no. individuals analyzed	No. Reps.	mg/g dry weight (± 95% confidence limits)			
				Calcium	Magnesium	Potassium	Sodium
1971							
June 17—20		27	5	1.40 ± 0.47	1.17 ± 0.14	7.71 ± 0.91	2.81 ± 0.18
July 1		15	3	3.63 ± 4.66	1.83 ± 1.64	8.33 ± 2.28	3.62 ± 1.27
July 21—27		4	1	1.14	0.72	4.92	2.28
Sept. 14	Old adults	14	3	1.85 ± 2.31	1.45 ± 2.40	3.98 ± 0.23	2.57 ± 1.81
	Teneral	4	1	2.66	7.19	11.54	9.54
1972							
June 14—16		14	2	2.21 ± 0.02	1.13 ± 0.64	4.54 ± 8.37	2.15 ± 0.17
Sept. 20		7	2	1.58 ± 5.33	0.71 ± 0.31	4.87 ± 1.39	2.44 ± 2.74
1974							
May 20	Teneral	7	1	2.79	1.38	10.44	2.65
	Soft*	6	1	1.70	0.99	7.38	2.49
	Old adults	8	2	0.98 ± 0.27	1.09 ± 4.76	5.21 ± 1.84	3.32 ± 7.99
June 26		19	4	1.39 ± 0.40	1.29 ± 0.11	7.50 ± 1.45	3.17 ± 1.96
July 22—Aug. 2		47	10	1.80 ± 0.75	0.92 ± 0.24	4.95 ± 0.41	2.51 ± 0.76
Oct. 21	Teneral	5	1	3.57	2.32	12.55	4.84

* Adults with soft elytra, all other adults are old (sexually mature) unless otherwise indicated.

Table 5. Biomass and standing crops of chemical elements in leaf fall, aspen woodland soil, and certain invertebrates from the Kananaskis Valley and biomass and standing crop in aspen soil from Alaska

	Nos./m²	Biomass mg/m²	mg/m² Ca	Mg	K	Na
Van Cleve and Noonan (1971)						
Litter	—	282.8×10^3	6.00×10^3	0.68×10^3	0.54×10^3	—
Fermentation	—	867.7×10^3	17.87×10^3	2.17×10^3	1.48×10^3	—
Humus	—	3051.7×10^3	40.28×10^3	7.93×10^3	6.41×10^3	—
Present Study						
Leaf fall	—	159×10^3	3.15×10^3	0.51×10^3	0.96×10^3	0.009×10^3
Litter	—	1058×10^3	31.44×10^3	2.06×10^3	2.14×10^3	0.053×10^3
Fermentation	—	2087×10^3	66.83×10^3	4.30×10^3	3.55×10^3	0.104×10^3
Humus	—	5947×10^3	159.32×10^3	6.60×10^3	21.53×10^3	7.34×10^3
Mycelia						
Litter	—	6.76×10^3	224.56	12.95	16.23	2.71
Fermentation	—	33.47×10^3	1111.03	63.58	80.32	13.39
Humus	—	43.62×10^3	1448.22	82.88	104.69	17.45
Maximum amounts in fungi during colonization		1420.7	47.18	2.70	1.70	0.57
Diplura	949	31.46	0.056	0.050	0.144	0.097
Oribatid mite						
Eupterotegaeus rostratus	520*	8.47	0.130	0.015	0.032	0.023
Carabid adults						
Total community	5.72	50.26	0.080	0.082	0.374	0.124
Calathus ingratus	1.01	7.23	0.008	0.007	0.058	0.018
Calosoma frigidum	0.05	7.10	0.012	0.019	0.065	0.016
Agonum retractum	3.70	15.45	0.021	0.017	0.085	0.035
Other stages of *A. retractum*	eggs	0.84	0.002	0.002	0.009	0.005
	larvae	4.66	0.011	0.013	0.050	0.002
	old adults and tenerals	20.95	0.048	0.038	0.146	0.077

* From Mitchell (1974)

and their food while high calcium levels in oribatid adults and in micro-fungal mycelia were also correlated (Fig. 1 and Table 2). On the other hand, another mycophage, the collembolan *Ceratophysella armata* NICOLET, had low calcium concentrations. The chemical composition of terrestrial invertebrates from this study and from studies in south-eastern U.S. ecosystems are summarized in Table 3. The data of REICHLE et al. (1969) were expressed in terms of ash-free dry weight but this fact does not affect conclusions of comparisons made between the various studies because the arthropods referred to in Table 3 were of low ash content. For example, mean ash content of *Agonum retractum* adults was 3.15 % ± 0.20 (S. E., n = 4) and was similar to REICHLE et al. mean of 4.97 % for carabid adults. The high potassium levels in lepidopterous larvae in this study compare with results from other studies (Table 3 and see FLORKIN and JEUNIAUX 1964). Basisiocarps also had high levels as did those examined by STARK (1973), AUSMUS and WITKAMP (1974) and CROMACK et al. (1975).

The carabid, *Agonum retractum*, was the only arthropod studied for chemical variation within and between age groups. Potassium was concentrated by eggs but the contributions of eggs to the chemical concentrations of gravid females would not have accounted for the high potassium levels in breeding females in 1971. Possibly, fluctuations in whole body concentrations of this chemical element were caused, in part, by initiation of feeding after overwintering and thereafter by changes in diet and by corresponding chemical changes in diet. The turnover rate of potassium by adults of *A. retractum* was more than 20 times that of calcium (CARTER and PRITCHARD 1976) but it is unlikely that potassium was in short supply or was limiting. However, in aphids trace amounts of magnesium, copper, iron and zinc were required for normal growth (DADD 1967). Fluctuations in whole body potassium in adult *A. retractum* may have reflected changes in availability and intake of trace elements.

Data on chemical standing crops for the soil horizons in the Kananaskis Valley were higher than those reported by VAN CLEVE and NOONAN (1971) for Alaskan soil and in large part reflect the greater biomass of soil in the former site (Table 5). Biomass and standing crops of chemical elements of the oribatid *E. rostratus* were certainly a small proportion of those of the total oribatid community because this species accounted for approximately 0.4 % of the total oribatids in the aspen woodland site (MITCHELL 1974). By contrast, the mean density, biomass and chemical standing crops of the carabid *A. retractum* was approximately 64 %, 31 % and between 23—31 %, respectively, of those of adults of the total carabid community (from Table 5).

The roles of particular consumers in chemical cycling may be described if data on their chemical concentrations and chemical standing crops are combined with estimates of rates of ingestion and rates of elimination of chemical elements by the consumers. To date, such information is only available for the carabid *Agonum retractum* and for the oribatid *Eupterotegaeus rostratus*. Adults of *A. retractum* ingested and recycled (via egestion, mortality and oviposition) 0.035 mg and 0.82 mg/m²/month of calcium and potassium, respectively, during their main period of activity (CARTER and PRITCHARD 1976) while adults of *E. rostratus* ingested 0.112 mg of calcium and 0.015 mg potassium per m² during peak feeding (CARTER 1975). However, the latter species was but one of many mycophages which occurred in the aspen soil and which included other oribatids (see above), collembola, and enchytraeids (DASH and CRAGG 1972). In addition, oribatids such as *E. rostratus*, fed for longer periods of time than did carabids.

The role of the fungi in chemical cycling is poorly understood. There are data available on rates of colonization of freshly fallen litter by fungi and on the amounts of chemical elements immobilized in fungal biomass during colonization (VISSER and PARKINSON, in press). The amounts at peak immobilization are reported in Table 5. These figures are low in comparison with chemical standing crops in soil fungi in the various horizons and in comparison with chemical input through leaf fall (Table 5). However, the former figures were based only on standing crops of chemical elements in fungal mycelia on freshly fallen litter and thus do not indicate the extent of chemical flow through the fungi.

6. Summary · Zusammenfassung

Concentrations and standing crops of four chemical elements in soil arthropods and their surroundings in an aspen woodland ecosystem in the Kananaskis Valley of Alberta are reported. Calcium concentrations ranged from 1.1—2.1 mg/g dry wt, for the majority of arthropods, to 108.4 mg/g for stratiomyid larvae and millipedes, both with highly calcareous exoskeletons. Potassium levels in arthropods were highest in lepidopterous larvae, 33.5 mg/g. Generally, the chemical concentrations of consumers were independent of their feeding habits and appeared instead to be dependent on biochemical and physiological characteristics of different taxa.

In the carabid *Agonum retractum* Leconte, potassium levels were highest in eggs, larvae and teneral adults (10.3—11.5 mg/g dry wt) and in females decreased significantly after June. Eggs and tenerals had the highest sodium content (5.7—6.0 mg/g). Standing crops of calcium, magnesium, potassium and sodium in *A. retractum* were 0.048, 0.038, 0.146 and 0.080 mg/m² respectively, while in adults of the oribatid *Eupterotegaeus rostratus* Higgins and Woolley were 0.130, 0.015, 0.032 and 0.023 mg/m². The mean density and biomass of *A. retractum* accounted for 64% and 31% respectively of the total adult carabid community, whereas the oribatid accounted for only 0.4% of the total adult oribatids in the aspen soil.

Konzentrationen und „Standing Crops" von Kalzium, Magnesium, Kalium und Natrium in boden- und streubewohnenden Arthropoden und ihrer Nahrung in einem Espenwald-Ökosystem in den Rocky Mountains (Kanada)

Über Konzentrationen und „Standing Crops" von 4 chemischen Elementen in Boden-Arthropoden und ihrer Umgebung in einem Espenwald-Ökosystem (im Kananaskis-Tal in Alberta) wird berichtet. Die Kalzium-Konzentrationen schwanken bei der Überzahl der Arthropoden von 1,1 bis 2,1 mg/g Trockengewicht; bei Stratiomyiden-Larven und Tausendfüßlern, die ein kalkreiches Exoskelett besitzen, werden Gehalte von 108,4 mg/g Trockengewicht erreicht. Die K-Gehalte von Arthropoden waren mit 33,5 mg/g bei den Lepidopteren-Larven am höchsten. Allgemein schienen die Mineralgehalte der Konsumenten von ihrer Ernährungsweise unabhängig zu sein und statt dessen von biochemischen und physiologischen Besonderheiten der verschiedenen Taxa beeinflußt zu werden.

Bei dem Carabiden *Agonum retractum* Leconte waren die K-Gehalte in den Eiern am höchsten; Larven und frisch geschlüpfte Adulte enthielten 10,3—11,5 mg/g Trockengewicht und bei Weibchen nahm der K-Gehalt nach dem Monat Juni signifikant ab. Eier und frischgeschlüpfte Tiere hatten den höchsten K-Gehalt (5,7—6,0 mg/g). Die „Standing Crops" von Kalzium, Magnesium, Kalium und Natrium betrugen bei *A. retractum* 0,048, 0,038, 0,146 bzw. 0,080 mg/m², während sie bei den Adulten der Oribatiden-Art *Eupterotegaeus rostratus* Higgins et Woolley 0,130, 0,015, 0,032 und 0,023 mg/m² betrugen. Die durchschnittliche Besatzdichte und Biomasse von *A. retractum* betrug 64% bzw. 31% der gesamten adulten Carabiden-Gemeinschaft, während der Besatz mit *E. rostratus* nur 0,4% des gesamten adulten Oribatidenbesatzes im Espenwald-Boden ausmachte.

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